

A MODEL FOR THE MORPHOGENESIS OF RIBS IN AMMONITES INFERRED FROM ASSOCIATED MICROSCULPTURES

by ANTONIO CHECA

ABSTRACT. Eight morphological types of microsculpture have been recognized on the outer shell surface of well-preserved ammonites. They consist mainly of wrinkles and creases which were developed on a pliant material. They are interpreted as the result of compressive stresses which occurred on a free (i.e. uncalcified) periostracum. This is the first evidence of periostracal development in ammonoids, and its relation to the shell suggests a mode of calcification similar to present-day molluscs. This periostracum was also attached to the soft body along longitudinal lines. All microsculptures were compression structures. This, their concentration within intercostal valleys, and additional evidence, leads to the proposal of a new morphogenetic model for ammonite ribs, in which they represent compression folds developed on the free periostracum which were later calcified. Evidence that ribs coincide with growth halts supports this view. An enigmatic feather-like ornament is interpreted merely as a long-wave variant of wrinkling. The study of shell structure implies that the aperture was never fully calcified except at maturity. Therefore, ribs did not reinforce the apertural edge, which was easily torn allowing the ammonite to scape, but rather avoided the peeling of the shell from some distance to the aperture backwards. Differences in timing and mode of calcification existed between constricted and non-constricted ammonites. In fact, the presence of constrictions could indicate episodic growth, similar to that of some Recent gastropods.

AMONG the many varieties of ammonoid ornaments, ribs are the most important elements. They are found from the Palaeozoic onwards, and gained in strength with time (Ward 1981). Despite their structural importance, very few studies have dealt with costal morphogenesis. The only previous morphogenetic study is that by Checa and Westermann (1989) who recognized that, in general, growth lines are perfectly parallel to ribs in Jurassic ammonites, so that the peristome had to change its shape to accommodate the variable costal morphology. These authors called this the segmental growth pattern.

The examination of extremely well-preserved Jurassic and Cretaceous ammonites allowed me to recognize diverse superficial microsculptures, which were originally developed in the external surface of the shell, and arranged and associated in a precise manner. Their interpretation allows us to form a precise picture of the pattern of shell calcification in ammonites and to establish an unexpected model of construction of ribs, which is completely new to shelled invertebrates.

In this paper the term 'microsculpture' is used to describe variously shaped microreliefs developed on the outer shell surface and different from usual ornamentation, such as ribs or tubercles.

MATERIAL

Microsculptures were first observed by the author at the Oxford University Museum in 1989 in an extensive collection of Upper Jurassic *Pavlovia*, from a disused pit in Hartwell, south-west of Aylesbury, Buckinghamshire. Only twelve specimens displayed microsculptures, mainly for preservational reasons. Given the exceptional nature of this material, only one shell sample was studied under SEM, which revealed that the original microstructure had been retained. Microsculptures were also profusely observed in seven Hildoceratinae, one *Peronoceras* and one

TABLE 1. List of material, with indication of microsculpture(s) recognized (numbers refer to microsculpture description in the text). Specimens labelled C are housed at the Natural History Museum, London; those labelled J or JZ are at the Oxford University Museum. BMNH: Natural History Museum London; DPUG: Departamento de Estratigrafía y Paleontología de la Universidad de Granada; GPIUH: Geologisch-Paläontologisches Institut der Universität Hamburg.

Taxon	Age	Locality	Registration No.	Microsculpture
PHYLLOCERATINA				
Phyllocerataceae				
<i>Tragophylloceras ibex</i> (Quenstedt)	Pliensbachian	Watford (Northamptonshire)	C19581, C56638	(2)
<i>T. boblayei</i> (d'Orbigny)	Pliensbachian	Cheltenham (Gloucestershire)	C28215	(2)
<i>T. loscombi</i> (Sowerby)	Pliensbachian	Charmouth (Dorset)	C36714, -848, C55644, C73923, -5 C50451	(2)
<i>T. undulatum</i> (Smith)	Pliensbachian	Radstock (Somerset)		(2)
ANCYLOCERATINA				
Ancylocerataceae				
<i>Crioceratites seelevi</i> (Neumayr and Uhlig)	Hauterivian	Ihme (nr. Hannover)	C14392, -3, -4	(1)
Turrititaceae				
<i>Baculites chicoensis</i> Reeside	Campanian	Nanaimo (Vancouver Isl.)	C53070	(8)
AMMONITINA				
Psilocerataceae				
<i>Asteroceras confusum</i> Spath	Sinemurian	Bredon (Worcestershire)	C2223	(3)
<i>Caenites brooki</i> (Sowerby)	Sinemurian	Dorset	C47352	(3)
<i>Oxyntoceras</i> sp.	Sinemurian	—	Unreg. (BMNH)	(2)
Eoderocerataceae				
<i>Androgynoceras maculatum</i> (Young and Bird)	Pliensbachian	Dorset	C63410	(8)
<i>Oistoceras figuratum</i> (Simpson)	Pliensbachian	Kirton (Lincolnshire)	C73534	(1), (5)
<i>Amaltheus stokesi</i> (Sowerby)	Pliensbachian	Stroud (Gloucestershire)	C10380	(8)
Dactyloceratidae sp.	Toarcian	—	Ch. S ₁ (DPUG)	(4)
<i>Peronoceras</i> sp.	L. Toarcian	—	C67532	(5)
<i>Peronoceras</i> sp.	L. Toarcian	—	J31943	(1), (4), (5)
Hildocerataceae				
<i>Harpoceras falcifer</i> (Sowerby)	L. Toarcian	Northamptonshire	C68616	(2)
<i>Elegantoceras</i> sp.	L. Toarcian	nr. Hamburg	Unreg. (GPIUH)	(2)
<i>Pseudohioceras</i> sp.	U. Toarcian	—	Unreg. (BMNH)	(2)
<i>Pseudohioceras lithense</i> (Young and Bird)	U. Toarcian	Northamptonshire	C66917, -8, -9	(8)

<i>Ospertioceras</i> sp.	U. Toarcian	—	J30375	(2), (5)
<i>Hildoceras</i> sp.	L. Toarcian	—	J30359	(2)
<i>Hildoceras</i> sp.	L. Toarcian	—	J30356	(8)
<i>Hildoceras</i> sp.	L. Toarcian	—	J30352, -3, -5, -64	(2), (8)
<i>Hildaites</i> sp.	L. Toarcian	—	J30368	(2), (8)
<i>Letoceras</i> sp.	L. Aalenian	Goslar (Harz)	C4880	(2)
Stephanocerataceae				
<i>Kosmoceras castor</i> (Reinecke)	Callovian	—	C7932	(1)
<i>Gullielmites</i> sp.	Callovian	Twyford (Buckinghamshire)	C79439, -40	(8)
<i>Cardioceras</i> sp.	Oxfordian	—	JZ.2224	(8)
<i>Cardioceras</i> sp.	Oxfordian	Staffin (Skye)	C71044	(2)
<i>Amoeboceras rosenkrantzii</i> Spath.	U. Oxfordian	Staffin (Skye)	Unreg. (BMNH)	(2), (8)
<i>Dimorphinites</i> sp.	Bajocian	Yeovil (Somerset)	C52049	(8)
Perisphinctaceae				
<i>Proplanulites</i> sp.	Callovian	—	Unreg. (BMNH)	(8)
<i>Binatisphinctes</i> sp.	Callovian	Kowno (W. Russia)	C7983	(3)
<i>Dichotomosphinctes</i> sp.	Oxfordian	Staffin (Skye)	Unreg. (BMNH)	(3)
<i>Crussoliceras divisum</i> (Quenstedt)	L. Kimmeridgian	Zafarraya (Granada)	Ch.Z1.2b.1 (DPUG)	(5)
<i>Rasenia</i> sp.	L. Kimmeridgian	Market Rasen (Lincolnshire)	C69820	(1), (3)
<i>Rasenia</i> sp.	L. Kimmeridgian	Horncastle (Lincolnshire)	C69831	(3), (8)
<i>Rasenia</i> sp.	L. Kimmeridgian	Market Rasen (Lincolnshire)	C69832	(3), (8)
<i>Rasenia</i> sp.	L. Kimmeridgian	Market Rasen (Lincolnshire)	C70514	(1), (3), (8)
<i>Pararasenia</i> sp.	L. Kimmeridgian	Market Rasen (Lincolnshire)	C93899	(8)
<i>Pavlovia</i> sp.	Portlandian	Hartwell (Buckinghamshire)	J30355, -68, J35848,	(5)
			-68, -99	
<i>Pavlovia</i> sp.	Portlandian	Hartwell (Buckinghamshire)	J35894, -9	(4), (6)
<i>Pavlovia</i> sp.	Portlandian	Hartwell (Buckinghamshire)	J35857,	(1), (5)
			-87, -91	
<i>Pavlovia</i> sp.	Portlandian	Hartwell (Buckinghamshire)	J35883, -94	(3), (5)
Hoplitaceae				
<i>Hypacanthohoplites jacobii</i> (Collet)	Albian	Vöhrum (Hannover)	C14550	(3), (8)
<i>Placenticeras meeki</i> Boehm	U. Cretaceous	South Dakota	C22686, C40062	(2), (8)
<i>Placenticeras placenta</i> (Dekay)	U. Cretaceous	South Dakota	C31345, C74029	(2), (8)
<i>Placenticeras unkwelauensis</i> Klinger	Coniacian	Zululand	C93898	(2)
<i>Hoplites dentatus</i> (Sowerby)	Albian	Devizes (Wiltshire)	C88627	(7)
<i>Euthoplites</i> sp.	U. Albian	Calais	C92747	(2)

TABLE 1. List of material, with indication of microsculpture(s) recognized (numbers refer to microsculpture description in the text). Specimens labelled C are housed at the Natural History Museum, London; those labelled J or JZ are at the Oxford University Museum. BMNH: Natural History Museum London; DPUG: Departamento de Estratigrafía y Paleontología de la Universidad de Granada; GPIUH: Geologisch-Paläontologisches Institut der Universität Hamburg

Taxon	Age	Locality	Registration No	Microsculpture
PHYLLOCERATINA				
Phyllocerataceae				
<i>Tragophylloceras ibeyi</i> (Quenstedt)	Pliensbachian	Watford (Northamptonshire)	C19581, C56638	(2)
<i>T. boblayei</i> (d'Orbigny)	Pliensbachian	Cheltenham (Gloucestershire)	C28215	(2)
<i>T. loscouhii</i> (Sowerby)	Pliensbachian	Charmouth (Dorset)	C36714, -848, C55644, C73923, -5	(2)
<i>T. undulatum</i> (Smith)	Pliensbachian	Radstock (Somerset)	C50451	(2)
ANCYLOCERATINA				
Ancylocerataceae				
<i>Crioceratites seeleyi</i> (Neumayr and Uhlig)	Hauterivian	Ihme (nr Hannover)	C14392, -3, -4	(1)
Turnritaceae				
<i>Buculites chiconis</i> Reeside	Campanian	Nanaimo (Vancouver Isl.)	C53070	(8)
AMMONITINA				
Psilocerataceae				
<i>Asteroceras confusum</i> Spath	Sinemurian	Bredon (Worcestershire)	C2223	(3)
<i>Caenites brooki</i> (Sowerby)	Sinemurian	Dorset	C47352	(3)
<i>Oxyntoceras</i> sp.	Sinemurian	—	Unreg. (BMNH)	(2)
Eoderoceerataceae				
<i>Androgynoceras maculatum</i> (Young and Bird)	Pliensbachian	Dorset	C63410	(8)
<i>Ostoceras figulinum</i> (Simpson)	Pliensbachian	Kirton (Lincolnshire)	C73534	(1), (5)
<i>Anatthis stokesi</i> (Sowerby)	Pliensbachian	Stroud (Gloucestershire)	C10380	(8)
<i>Dactyloceratidae</i> sp.	Toarcian	—	Ch. S ₁ (DPUG)	(4)
<i>Peraioceras</i> sp.	L. Toarcian	—	C67532	(5)
<i>Peraioceras</i> sp.	L. Toarcian	—	J31943	(1), (4), (5)
Hildocerataceae				
<i>Harpoceras falctifer</i> (Sowerby)	L. Toarcian	Northamptonshire nr. Hamburg	C68616	(2)
<i>Elegantoceras</i> sp.	L. Toarcian	—	Unreg. (GPIUH)	(2)
<i>Pseudohoceras</i> sp.	U. Toarcian	—	Unreg. (BMNH)	(2)
<i>Pseudohoceras lithense</i> (Young and Bird)	U. Toarcian	Northamptonshire	C66917, -8, -9	(8)
<i>Osperletoceras</i> sp.	U. Toarcian	—	J30375	(2), (5)
<i>Hildoceras</i> sp.	L. Toarcian	—	J30359	(2)
<i>Hildoceras</i> sp.	L. Toarcian	—	J30356	(8)
<i>Hildoceras</i> sp.	L. Toarcian	—	J30352, -3, -5, -64	(2), (8)
<i>Hildites</i> sp.	L. Toarcian	—	J30368	(2), (8)
<i>Leioceras</i> sp.	L. Aalenian	Goslar (Harz)	C4880	(2)
Stephanocerataceae				
<i>Kosmoceras extor</i> (Reinecke)	Callovian	—	C7932	(1)
<i>Gulchinites</i> sp.	Callovian	Twyford (Buckinghamshire)	C79439, -40	(8)
<i>Cardioceras</i> sp.	Oxfordian	—	JZ.2224	(8)
<i>Cardioceras</i> sp.	Oxfordian	Staffin (Skye)	C71044	(2)
<i>Amoeboceras rosenkrantzii</i> Spath	U. Oxfordian	Staffin (Skye)	Unreg. (BMNH)	(2), (8)
<i>Dimorphinites</i> sp.	Bajocian	Yeovil (Somerset)	C52049	(8)
Perisphinctaceae				
<i>Propilamites</i> sp.	Callovian	—	Unreg. (BMNH)	(8)
<i>Bimittisphinctes</i> sp.	Callovian	Kowno (W. Russia)	C7983	(3)
<i>Dichotomiosphinctes</i> sp.	Oxfordian	Staffin (Skye)	Unreg. (BMNH)	(3)
<i>Crusolliceras divisum</i> (Quenstedt)	L. Kimmeridgian	Zafarraya (Granada)	Ch. ZI. 2b.1 (DPUG)	(5)
<i>Rasenina</i> sp.	L. Kimmeridgian	Market Rasen (Lincolnshire)	C69820	(1), (3)
<i>Rasenina</i> sp.	L. Kimmeridgian	Horncastle (Lincolnshire)	C69831	(3), (8)
<i>Rasenina</i> sp.	L. Kimmeridgian	Market Rasen (Lincolnshire)	C69832	(3), (8)
<i>Rasenina</i> sp.	L. Kimmeridgian	Market Rasen (Lincolnshire)	C70514	(1), (3), (8)
<i>Pararasenina</i> sp.	L. Kimmeridgian	Market Rasen (Lincolnshire)	C93899	(8)
<i>Portovia</i> sp.	Portlandian	Hartwell (Buckinghamshire)	J30355, -68, J35848, -68, -99	(5)
<i>Portovia</i> sp.	Portlandian	Hartwell (Buckinghamshire)	J35894, -9	(4), (6)
<i>Portovia</i> sp.	Portlandian	Hartwell (Buckinghamshire)	J35857, -87, -91	(1), (5)
<i>Portovia</i> sp.	Portlandian	Hartwell (Buckinghamshire)	J35883, -94	(3), (5)
Hoplitaceae				
<i>Hypacanthohoplites jacobi</i> (Collet)	Albian	Vöhrum (Hannover)	C14550	(3), (8)
<i>Pluenticeras meeki</i> Boehm	U. Cretaceous	South Dakota	C22686, C40062	(2), (8)
<i>Pluenticeras plicata</i> (Dekay)	U. Cretaceous	South Dakota	C31345, C74029	(2), (8)
<i>Pluenticeras unkwelmensis</i> Klinger	Coniacian	Zululand	C93898	(2)
<i>Hoplites dentatus</i> (Sowerby)	Albian	Devizes (Wiltshire)	C88627	(7)
<i>Euhoplites</i> sp.	U. Albian	Calais	C92747	(2)

Ospereioceras, from Toarcian black shales of southern England. All of these ammonites are fragmentary, and usually only an incomplete living chamber is preserved. Judging from phragmocone remains, these were not sediment-filled and became crushed and completely flattened during burial. Shells always display a typically iridescent appearance.

The huge collection of the Natural History Museum, London (c. 92 000 ammonites, Mr S. Baker, pers. comm.), was reviewed during 1991 in the search for new material. Only forty-nine specimens (ranging from Pliensbachian to Campanian in age) display similar and additional features. Among them, a collection of five *Rasenia* and *Pararasenia* from the English Oxford Clay is particularly important.

Additional material housed at the Department of Stratigraphy and Palaeontology (Universidad de Granada) and at the Geologisch-Paläontologisches Institut (Universität Hamburg), including two Triassic specimens, allowed complementary observations.

For evident reasons, shell damaging analysis (e.g. SEM) were kept to a minimum; therefore, tiny structures needing high magnification are illustrated as drawings, rather than as SEM photographs. A complete faunal list, together with the kind or kinds of microsculptures recognized, is provided in Table 1.

MICROSCULPTURES

Description

Microsculptures can be differentiated into eight morphological categories. A breakdown of the specific taxa showing these categories is shown on Table 1.

(1) *Longitudinal wrinkles* (Pl. 1, fig. 7; Pl. 4, fig. 5). These are tiny, closely spaced, low-relief wrinkles which appear at the intercostal valleys when ribs are more or less straight, and which fade out towards both rib slopes. They are without exception longitudinal, i.e., perpendicular to ribs.

(2) *Adorally convergent wrinkles* (Pl. 2, figs 2–5; Pl. 3, figs 4–5; Pl. 5, fig. 4; Pl. 6, fig. 3). They are homologous to the longitudinal wrinkles, but one developed exclusively between adorally concave (all along or in part) costae. Since they always tend to be perpendicular to ribs, their orientation changes along the flank, so as to converge towards the hypothetical centre of the rib arch. Interestingly, the enigmatic feather-like ornament recorded by other authors (see Arkel *et al.* 1957, p. L92) seems to be merely a 'giant' (long wavelength) variant of this kind of wrinkle (see below).

(3) *Wrinkles associated with concave primary ribs* (Pl. 1, fig. 3; Pl. 4, figs 2–6). They are found at the adoral slope of specially prominent concave primary ribs. In some specimens of *Rasenia* (Pl. 4, fig. 4) they originate at the crest of the rib, and converge slightly and vanish 'downslope'.

(4) *Dents and wrinkles on the ribs* (Pl. 1, fig. 5; Pl. 3, figs 6–7). These are more or less longitudinal features which give the ribs an irregular and deflated appearance. They are different from some low-

EXPLANATION OF PLATE 1

Figs 1–7. *Pavlovia* sp. Oxford University Museum; Hartwell, south-west of Aylesbury, Buckinghamshire; Portlandian. 1, J35857; ventral view, aperture to the top; triangular shaped kink (arrow) in an intercostal valley; $\times 1.4$. 2, J35868; aperture to the top; periumbilical pinches; $\times 1.5$. 3–4, J35894; oblique right and right views, aperture to the left; long radial kink at the adoral base of the third complete rib from the left, wrinkles on the concave side of primary ribs and periumbilical pinches; note also conspicuous growth lines at the adoral slope of ribs; $\times 2$. 5–7, J35899; left, right and oblique left views; dented ribs, radial kinks, specially in 6, and longitudinal wrinkles in 7; 5–6, $\times 1.6$; 7, $\times 2.2$.

All specimens coated with ammonium chloride.



relief lines crossing the rib fold (microsculpture 8), given their irregularity and their absence of homology.

(5) *Creases with kink profile* (Pl. 1, figs 1, 3–6; Pl. 3, fig. 6). They consist of intercostal, radially-elongated irregular creases with angular profile, comparable to kinks or chevron folds. They are very commonly found in *Pavlovia*, in which they can have zigzag traces in plan-view and are most commonly found at the adoral bases of ribs, specially in acute intercostal folds.

(6) *Pinches along the umbilical seam* (Pl. 1, figs 2–3). They are exclusive to the strongly-ribbed *Pavlovia* and can be described as high-relief, small folds running along the adoral slopes of the wavy intersection between the spiral tube and the ribs of the previous whorl. Judging from their aspect they seem to represent squeezing of the soft body against the ribs of the preceding whorl.

(7) *Simious wrinkles at the venter* (Pl. 6, figs 1–2). This feature has only been recognized in one specimen of *Hoplites dentatus*, in which a more or less continuous arrangement of narrow wrinkles adapts to the basal ventral outline of the ventrolaterally coarsened radial ribs.

(8) *Low-relief longitudinal lines or smooth longitudinal strips, and associated arcuate wrinkles* (Pl. 2, figs 2–3; Pl. 4, figs 1–2, 5–6; Pl. 5, figs 1–2, 5). This is the most common and widespread kind of feature and seems to be independent of the ribbing pattern. It consists usually of narrow longitudinal (spiral) lines with slightly negative relief which are restricted, with some exceptions, to the intercostal valleys. These lines can have discontinuous tracings in the sense that they disappear and reappear intermittently when crossing either ribs or their valleys. This is the only microsculpture displaying homology over consecutive ribs. In some instances (in *Gulielmites*, *Baculites* and *Androgynoceras*, for example) low-relief lines are substituted by smooth bands. Sets of wrinkles may be found associated with low-relief lines or smooth bands. They are adorally-convex or chevron-like in plan view and are concentrically arranged, as if they hung from consecutive low-relief lines, in a 'drapery-like' fashion. In other instances, wrinkles are absent.

Interpretation

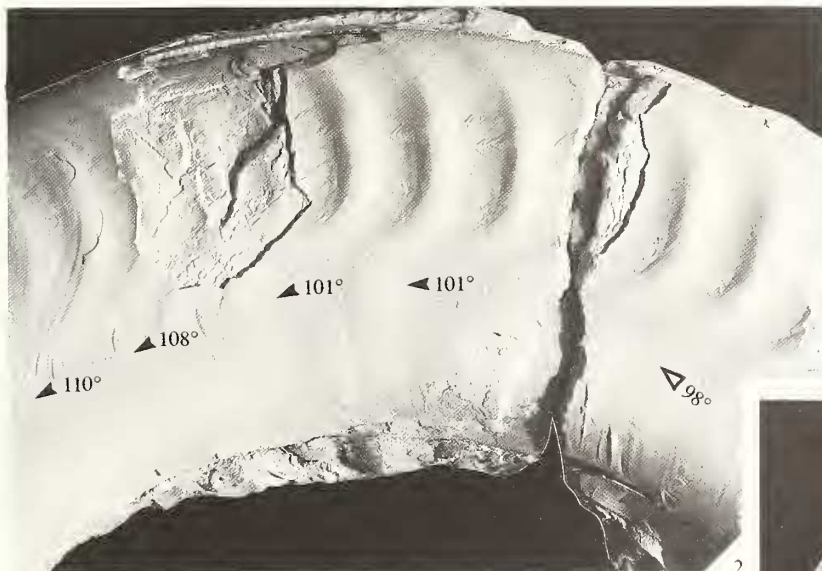
The existence of a free periostracum. In general, all of the observed features, except for type (8), seem to be products of non-fragile deformation of a flexible material. Therefore, none of them will have resulted from cracking of the shell during burial. Some cracks of taphonomic origin (Pl. 3, fig. 5) can be easily recognized by their fragile style. Microsculptures are also quite different from repaired injuries (e.g. see Hölder 1955, 1970; Guex 1967, 1968; Bayer 1970; Lehmann 1981; Landman and Waage 1986).

EXPLANATION OF PLATE 2

Figs 1–3. *Hildaites* sp. Oxford University Museum, J30368; locality unknown; lower Toarcian. 1, ventral view, aperture to the left; nacreous lamellae plunging apically; $\times 1.5$. 2–3, right view; adorally convergent wrinkles at the upper flank and low relief longitudinal lines and conspicuous associated wrinkles; note also non-congruence of ribs and growth lines; numbers in 2 are the angles formed by growth lines at the lateral sinus (see text); 3 is a composite photograph; 2, $\times 1.5$; 3, $\times 1.7$.

Figs 4–5. *Hildoceras* sp. Oxford University Museum; locality unknown; lower Toarcian. 4, J30359; oblique left view, adorally convergent wrinkles; $\times 1.9$. 5, J30353; left view, complexly arranged adorally convergent wrinkles; $\times 1.8$.

All specimens coated with ammonium chloride.



Given their ductile appearance, the most likely hypothesis is that the many rib-associated microsculptures occurred in life, in a non-calcified shell, that is, after secretion of the organic shell (periostracum) by the mantle lobe and before, or immediately after, the periostracum began to calcify. This is the so-called free periostracum. In present-day molluscs the free periostracum is a thin, pliable, fibrous layer which bears the growth lines and serves as a matrix for the deposition of calcium carbonate crystals. The fluid-filled extrapallial space separates the periostracum from the soft body. Calcification begins some way back after the periostracum is extruded by the mantle margins (periostracal groove; see Saleuddin and Petit 1983 and Text-fig. 3). Although Miller *et al.* (1957) supposed that the ammonite shell must have included a periostracal layer, its existence had not been recognized in previous studies on the shell structure (e.g. see Howarth 1975; Kulicki 1979; Birkelund 1980). This is, to my knowledge, the first evidence of a widespread free periostracum stage in ammonoids. Therefore, there are no reasons to assume different modes of calcification in ammonites and in present-day molluscs. The fact that growth lines (and, hence, the periostracum) were formed prior to wrinkling is evident, since growth lines, which were discontinuities on the periostracum, served usually as nucleation lines for wrinkles of types (1), (2) and (5) (Pl. 2, figs 2–3, 5; Pl. 6, fig. 3). In other instances wrinkles of type (2) only span the space between consecutive growth lines (Pl. 2, figs 2–3; Pl. 5, fig. 1; Pl. 6, fig. 3). A casual transversal break in the shell of a *Pavlovia* (Text-fig. 1A) crosses a radial kink and an associated small radial break; it can be appreciated how both features are immediately mitigated inwards of the shell, so that they had to be formed when the shell was less than one-twentieth of its final thickness.

Compressional microsculptures. In Recent molluscs the free periostracum is usually a flexible thin film. Although I have not found detailed studies of its mechanical properties, independently of its degree of tanning, the periostracum can be classified as a viscoelastic material, such as, for example, insect cuticle. Viscoelastic materials increasingly deform under tensile or compressive stress; once the stress is removed, recovery is also gradual, so that any measurement of strain is time-dependent (see Wainwright *et al.* 1976, fig. 2.12).

With the exception of type (8), all the other microsculptures are very similar in morphology to compressional features. In fact, types (5) and (7) are typical features resulting from Brazier-type buckling. This is a short-wave mode of buckling, typical of thin-walled cylinders, which are compressed axially (see Gordon 1978); in these conditions, a crease or crumple will develop when the stress in the skin is equivalent to:

$$\frac{1}{4}E\frac{t}{r},$$

being: E , Young's modulus, t , wall thickness and r , tube radius. We should remember that Young's modulus is the ratio of stress to strain and is constant for linearly elastic (Hookean) materials. The

EXPLANATION OF PLATE 3

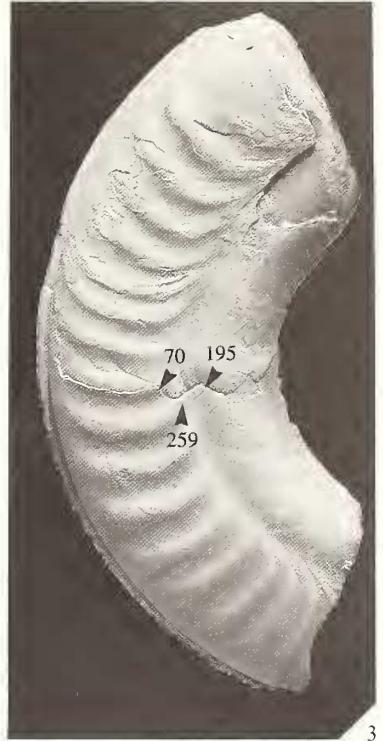
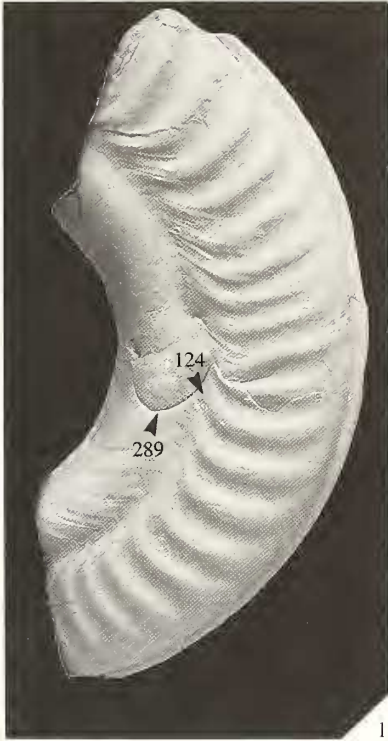
Figs 1–3. *Hildoceras* sp. Oxford University Museum, J30364; locality unknown; lower Toarcian; right, ventral and left views; repaired predatory injury, numbers refer to thickness (in μm) of the abandoned shell edge at different sites; $\times 1.5$.

Figs. 4–5. *Osperleioceras* sp. Oxford University Museum, J30375; locality unknown; upper Toarcian; left view; adorally convergent wrinkles; 4, $\times 3$; 5, $\times 1.3$.

Fig. 6. *Peronoceras* sp. Oxford University Museum, J31943; locality unknown; lower Toarcian; right view; dented ribs, longitudinal wrinkles; note also the 'deflated' appearance of the shell; $\times 1.8$.

Fig. 7. *Dactylioceratidae* sp. Departamento de Estratigrafía y Paleontología, Universidad de Granada, Ch.S₁; locality unknown; Toarcian; ventrolateral right view; dented ribs; $\times 5.5$.

All specimens coated with ammonium chloride.



probability of Brazier buckling is thus greater as the wall thins proportionally to tube radius and for low-stiffness (low E) materials. Therefore, microsculptures (5) and (7) could well have developed on a thin, non- to incipiently calcified periostracum, under compressive stress. The fact that in some specimens of *Pavlovia* some kinks developed into small, inverse fault-like cracks (Text-fig. 1A) can be explained by invoking a slightly calcified periostracum; this would be more likely to crack (that is, it behaved like a linearly elastic material) than if it was not calcified at all. Since the periostracum usually calcifies progressively as it leaves the apertural edge, these differences in calcification may also imply distance to the mouth.

Type (4) dents are typical of small defects acquired during the folding process. These can be demonstrated by attempting to fold a large piece of paper on a planar surface by pushing at both ends, which result in several wrinkles parallel to the stress direction rather than smoother folds.

Longitudinal (1) and adorally convergent wrinkles (2) can also be explained in a compressional context if some contraction occurred along the intercostal valley, transversal to the main compressional stress. Just imagine the uncalcified shell as a more or less smooth spiral tube which contracted longitudinally, so that a series of anticlines (ribs) and synclines (valleys) formed. The cross-sectional perimeter then enlarged along the rib height and diminished along the valleys; circumferential shortening within the intercostal valleys must be compensated for by wrinkling the periostracum. Adorally convergent wrinkles represented the same situation for concave ribs. Microsculptures (1) and (2) can be easily reproduced in the laboratory by adapting a thin plastic film to a surface modelled like ribbed ammonite flanks. Both in the cases of radial and concave ribs adaption (i.e. compression) of the film gave rise to the expected longitudinal (Text-fig. 2A) and adorally convergent wrinkles (Text-fig. 2B) respectively. In plasticine models wrinkles are much wider than in ammonites, since the plastic film is surely thicker than the ammonite periostracum was. According to Biot *et al.* (1961), when a layer (of viscosity μ_1) embedded in a less viscous medium (μ_2) is folded by lateral contraction, the dominant wavelength of the folds is given by:

$$2\pi t \sqrt[3]{\frac{\mu_1}{6\mu_2}}$$

t being the thickness of the layer. This formula could partly hold for ammonite periostracum, lined internally by the soft body through the extrapallial space. The whole pattern of wrinkles obtained experimentally is also much more irregular than ammonitic patterns, probably because the existence of longitudinal attachment lines of the soft body to the periostracum (see below) contributed to an ordered folding and wrinkling.

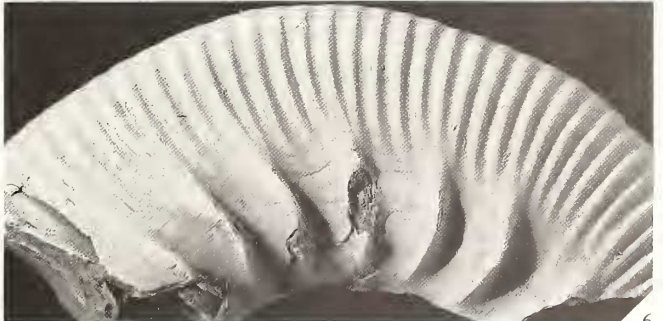
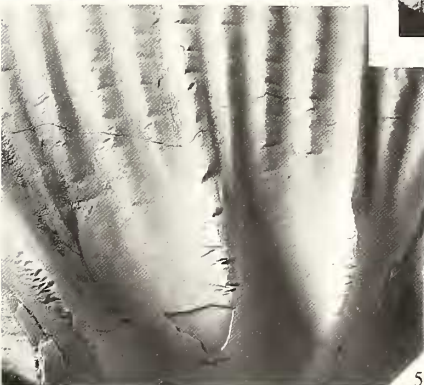
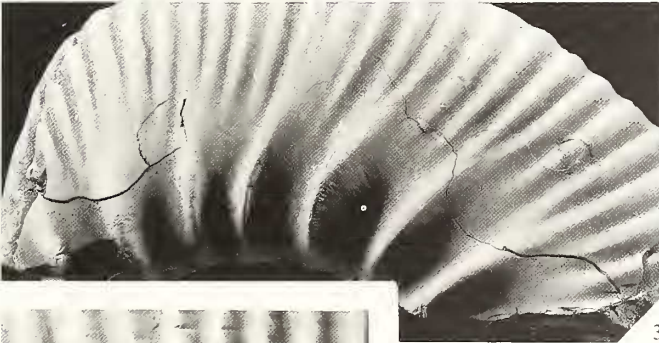
The ammonitic periostracum was also much less intensively wrinkled than expected in plasticine experiments, given the foreseeable radial shortening along the valleys between ribs (compared with laboratory models). This implies that the periostracum was also probably inflated elastically at the ribs, which agrees with its supposed viscoelastic behaviour.

EXPLANATION OF PLATE 4

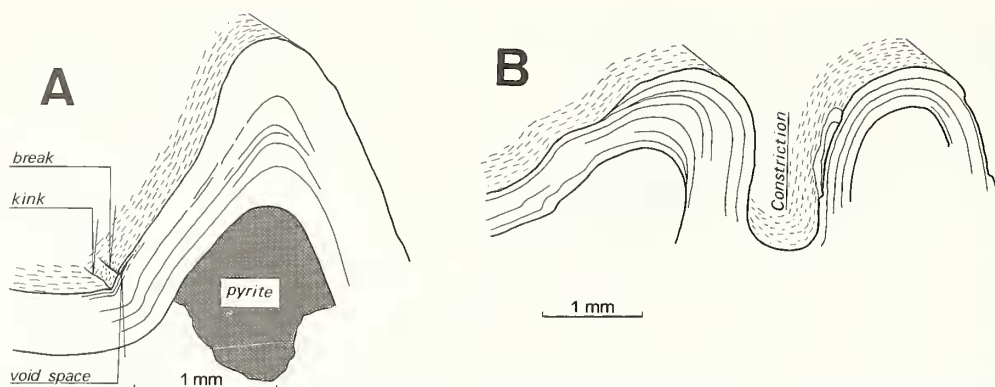
Figs 1–2. *Pararasenia* sp. Natural History Museum, C93899; Market Rasen, Lincolnshire; Lower Kimmeridgian; ventral and left views; primary ribs disappear after the injury and secondary ribs become smooth and widely spaced; note also high-relief longitudinal lines; $\times 1$.

Figs 3–6. *Rasenia* sp. Natural History Museum. 3, C69831; Horncastle, Lincolnshire; Lower Kimmeridgian; left view; more concave ribs display better developed wrinkles; $\times 1$. 4, C69820; Market Rasen, Lincolnshire; Lower Kimmeridgian; left view; wrinkles associated with concave primary ribs; $\times 5$. 5, C70514; Market Rasen, Lincolnshire; Lower Kimmeridgian; right view; wrinkles associated with concave primary ribs, longitudinal wrinkles in intercostal valleys and low-relief longitudinal lines at rib heights; $\times 2.5$. 6, C69832; Market Rasen, Lincolnshire; Lower Kimmeridgian; right view; wrinkles on concave primary ribs and low-relief longitudinal lines with associated wrinkles; $\times 1$.

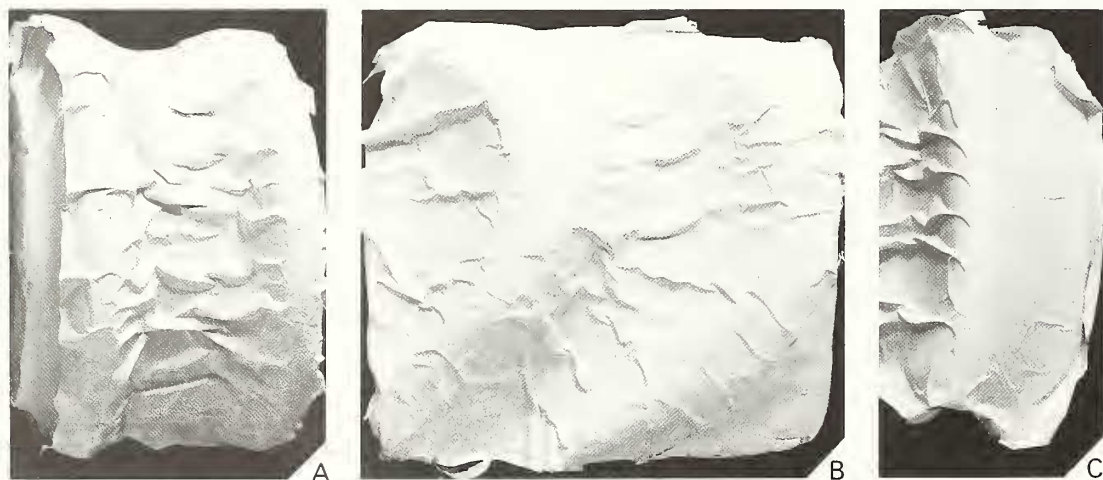
All specimens coated with ammonium chloride.



CHECA, *Pararasenia*, *Rasenia*



TEXT-FIG. 1. Camera lucida drawings of shell sections of *Pavlovia* sp., from specimens at the Oxford University Museum; Hartwell, south-west of Aylesbury, Buckinghamshire; Portlandian. A, J35891; radial kink and associated break developed at the base of the adoral slope of a rib; deformation was restricted to the outermost shell and the more internally secreted shell was not folded, although it accommodated to the previous kink. B, J35883; internal distribution of lamellae; after the constriction, shell lamellae fade out at the subsequent rib and are replaced by new lamellae growing under the rib (see also Text-fig. 4). Growth direction is to the left in both cases.



TEXT-FIG. 2. Laboratory reproduction of selected microsculptures; $\times 0.75$. A, intercostal longitudinal wrinkles, microsculpture (1). B, adorally convergent wrinkles, microsculpture (2). C, wrinkles developed at the concavity of primary ribs, microsculpture (3). In A and B a plastic film was adapted to a previously modelled surface; in C the plastic film was attached onto a straight rib which was subsequently curved.

In the reticulated surface of *Amaltheus* shells (Pl. 5, fig. 1), wrinkles appear along the diagonals of quadrangles formed by the intersection of low-relief longitudinal lines (8) and growth lines. These are interpreted as adorally convergent wrinkles modified by the intersection with a grid originally formed on the periostracum.

Wrinkles associated with concave primary ribs (3) are also compression features developed in a pliable skin when a previous fold is folded again along an axis transversal to the previous folding axis, but contained in the same axial plane. Just adapt a plastic sheet to a folded surface and try now

to curve the hinge of the fold. Wrinkles vanishing outwards from the fold will develop in the concave slope (Text-fig. 2C). This agrees with the fact that in some specimens of *Rasenia* in which primary ribs display different degrees of concavity, wrinkles gain in development with increasing concavity of the primary rib (Pl. 4, figs 3–4).

Periumbilical nips (6), even though compressional, are different from the above features in that they seem to have been developed on a purely elastic material. In two specimens of *Pavlovia* (Pl. 1, figs 2–3), periumbilical nips sometimes continue backwards into the primary ribs through tiny ridges. In these cases features of types (3) and (6) may have resulted from the same retraction episode of the soft body; in this way, no backwards motion actually occurred at the umbilical seam, in which the soft body became adpressed against the dorsum, leading to periumbilical nips. The fact that periumbilical nips seem to have developed in a highly elastic material may imply closeness to the apertural edge. Retraction took place progressively away from this seam, which made the primary ribs arch at the same time they were formed (Text-fig. 6C). Another area involved in this process was the dorsum. Attachment of the soft body to the dorsal area took place probably through the wrinkle layer (Walliser 1970; Bayer 1974; Doguzhaeva and Mutvei 1986).

Longitudinal lines and associated arcuate wrinkles. This feature is similar to the ones described above, in that it was also developed in a non-calcified periostracum in an apertural or near-apertural position (since no breaks are associated). The 'drapery-like' appearance of these structures provides a very suggestive clue to their origin. The most immediate explanation is that low-relief lines or smooth longitudinal bands were attachment lines of the periostracum to the soft body, whereas the periostracum between them was unattached and free to bulge and wrinkle by radial contraction along the intercostal valley (as in hildoceratins; see below). In a large specimen of *Hildaites*, wrinkles fade out with the disappearance of ribs towards the end of the living chamber (Pl. 2, fig. 2), which gives evidence of their relation to periostracum compression and bulging. The fact that homologous lines appear over several consecutive ribs implies that they are not casual effects; they were probably thin elongated tissular connections which, with growth, left a spiral trace on the periostracum (and, hence, on the shell).

When chevron wrinkles are specially well developed (Pl. 2, figs 2–3) it can clearly be appreciated how they are distributed into two sets forming an angle of some 90° , that is at $\pm 45^\circ$ of the foreseeable longitudinal shear stresses developed on the uncalcified periostracum (Text-fig. 3). Creases arranged in this fashion are the result of tensile and compressive stresses in directions at 45° to the plane of shearing, forming what is called by engineers a 'Wagner tension field' (Gordon 1978). The resultant arrangement of wrinkles is comparable to what is known as 'drape' in the textile trade. It is dependent on the shear modulus or modulus of rigidity G of the material, which is the ratio of shear stress to shear strain and represents the stiffness of the material in shear. On the whole, the higher the shear modulus of a material, the greater its tendency to creasing. The fact that the best developed wrinkles have been found in the big specimen of *Hildaites* implies that probably the periostracum in this specimen displayed an unusually high rigidity (high G). A likely hypothesis is that periostracum thickness (and hence stiffness) increased with size of the ammonite, so that at great diameters it tended to crease by shear. Smaller-sized individuals of *Hildoceras* do not display arcuate wrinkles, which can be related to the fact that their periostracum was thin enough to get a closer and more flexible fit to the soft body shape when folding occurred.

In some ammonites (e.g. *Rasenia*), low relief lines are well developed over the rib heights (which have a general appearance of deflation) and absent in the valleys (Pl. 4, fig. 5). In other cases they appear exclusively at the valleys, whereas ribs are neatly inflated (Pl. 2, figs 2–3). This implies that differential attachment could have taken place at different sites in different ammonites.

Analogous structures have been reported in acrotretoid brachiopods by Williams and Holmer (1992), who called these drapes (arcuate wrinkles) and nick points (lines of union of wrinkles). They supposed that nick points coincided with insertions of setal muscles, so that at these sites the forward growth of the shell was reduced compared to drapes. Evidently, this origin is unlikely for ammonites.

SHELL SECRETION MODE AND THE CONSTRUCTIONAL MORPHOLOGY OF APERTURES

Periodicity of rib formation

The above data imply that ribs were compressional features in the most strict sense. Complementary data about this mode of construction come from the study of other features which, in general, suggest that ribs were constructed in independent cycles of growth and compression.

In some *Pavlovia*, radially elongated kinks are found at the adoral base of each rib, specially at the ventral area (Pl. 1, figs 3–7; Text-fig. 1A). Conspicuous growth lines are also developed at this adoral slope. The basis of this slope could have constituted at some moment the boundary between a slightly calcified and a non-calcified shell; this discontinuity within the material was probably the most appropriate site for kink formation, since stresses could not have been easily transferred apicalwards of the shell. Inverse local kinks were also detected in one *Oistoceras fibulinum* (Pl. 5, fig. 5) at the apical slope of ribs, coinciding with marked growth lines.

Megastriations (*mégastries*) were defined by Bucher and Guex (1990) in some Triassic ammonoids as sites of periodic shell resorption. Interestingly, they invariably follow the apical limit of ribs, except for some intercalary and simple ribs (Bucher and Guex 1990, figs 3, 6). Therefore, the compressional mode of rib formation could have been present already in Triassic ammonoids, even though associated microsculptures have not yet been recognized.

A large specimen of *Hildaites* (Pl. 2, figs 2–3) displays spaced, low-relief radial lines at the lower flank; at two-fifths of the flank height they become retroverse, thus forming a lateral sinus, and develop into conspicuous growth lines which run upwards to join the ribs. These lines and their associated striations are much more developed and quite distinct from usual growth lines, and seem to correspond to growth halts. They tend to disappear towards the end of the body chamber, coinciding with mature weakening of the ribs. I have measured the apical angle formed by these striations and their backwards projections along the specimen and found it to increase significantly (by some 10°) with rib weakening towards the aperture. Four values (out of thirty-three) for this angle are provided in Plate 2, figure 2. This is consistent with the fact that the periostracum was differentially retracted and folded at the ribs; local retraction made the retroverse branch of striations rotate clockwise, such as they appear in Plate 2, figures 2–3, approaching the lower, radial branch and narrowing the angle between them. Since ribs (and hence retraction) tended to disappear towards the final mouth, the original, high-angled traces remained undeformed here.

EXPLANATION OF PLATE 5

- Fig. 1. *Amaltheus stokesi* (Sowerby). Natural History Museum, C10380; Stroud, Gloucestershire; Pliensbachian (Margaritatus Zone); left view; reticulated surface of the shell with diagonal wrinkles which are interpreted as a variant of adorally convergent wrinkles; $\times 2$.
- Fig. 2. *Baculites chicoensis* Reeside. Natural History Museum, C53070; Nanaimo, Vancouver Island; Campanian; left view; sets of adorally convex wrinkles with interspersed smooth bands on an intermediate shell layer; note the extremely wrinkled appearance of the outer shell surface preserved at the left bottom; $\times 1.5$.
- Fig. 3. *Cardioceras* sp. Natural History Museum, C71044; Trotternish, Staffin, Isle of Skye; Oxfordian; right view; growth lines cross ribs at the upper flank, near the ventral keel; $\times 4$.
- Fig. 4. *Tragophylloceras boblayei* (d'Orbigny). Natural History Museum, C28215; Cheltenham, Gloucestershire; Pliensbachian (Ibex Zone); left view; thin adorally convergent wrinkles; $\times 1.5$.
- Fig. 5. *Oistoceras figulinum* (Simpson). Natural History Museum, C73534; Kirton in Lindsay, Lincolnshire; Pliensbachian (Davoei Zone); ventral view, aperture to the top; well-marked growth lines, sometimes developing locally into inverse kinks, at the apical slope of ribs and high-relief longitudinal lines; $\times 2$.
- All specimens coated with ammonium chloride.



CHECA, *Amaltheus*, *Baculites*, *Cardioceras*, *Tragophylloceras*, *Oistoceras*

Modes of calcification

The model presented here implies that the periostracum was, to some extent, secreted intermittently and that its calcification must have been intermittent. Accordingly, I have searched for evidence of internal cyclicity within the shell. The only data in this respect are provided by Bucher and Guex (1990), who found megastriations to be the external intersection of two superimposed shell layers. Data gathered from the material studied show that this figure is general, although in detail two modes of timing in shell secretion can be distinguished, according to whether constrictions are present or not.

Non-constricted forms. In *Hildaites* and *Hildoceras* there is evidence that the apertural area took the form of an acute wedge in longitudinal cross-section, and therefore, the thinnest part of the shell at any moment of growth (except, possibly, for the final aperture). In the large specimen of *Hildaites*, the outer (nacreous) shell had been severely eroded at several places revealing the internal distribution into lamellae (Pl. 2, fig. 1). These are clearly imbricated, plunging apically, and each lamella apparently departs from one growth line. Kulicki (1979, pl. 47, fig. 7) found similarly arranged discontinuities within the shell of the Callovian genus *Quenstedtoceras*. In one *Hildoceras* (Pl. 3, figs 1–3) the aperture was severely injured by predation before maturity and the old damaged aperture remained exposed since the newly produced shell initiated under the old one. Shell thickness was measured at several points of the old aperture using a binocular microscope, attached to a Sony Magnescale unit for measuring stage displacement, with a precision of 1 μ m. Measurements revealed an increasing shell thickness from the very edge apicalwards. I should point out the extreme apertural thinness at the moment of the injury. Other small injuries in *Hildaites* (Pl. 2, fig. 2) and *Hildoceras* (Pl. 2, fig. 4) reveal the same pattern.

Constricted forms. In specimens of the genus *Pavlovia*, constrictions are rather numerous and they are typically developed every two or three complete primary ribs (plus the corresponding secondary and, eventually, intercalary ribs). The secretion pattern here is very different from that of hildoceratins, since the adoral slope of each rib formed immediately after the constriction marked the end of a shell secretion cycle. Here, the well marked surficial growth lines continue into the shell as lamellae extending backwards and wedging out under the rib, limiting the previous constriction adorally (Text-figs 1B, 4). Therefore the sector occupied by two successive constrictions corresponds to cycles of shell secretion. In *Pavlovia*, then, after the complete corrugated margin was thickened at the last-formed constriction, the body advanced rapidly while secreting a (slightly folded?) periostracum, which at this stage was only slightly, if at all, calcified. Repeated folding of the periostracum led to new ribs and growth stopped somewhat beyond the last calcified shell, when a new constriction was to be formed (Text-fig 6B). The animal secreted several parallel lamellae under the new shell until a thickened, fully calcified shell and aperture (constriction and subsequent rib) were obtained, when a new cycle was initiated. Therefore, the mode of shell secretion was episodic,

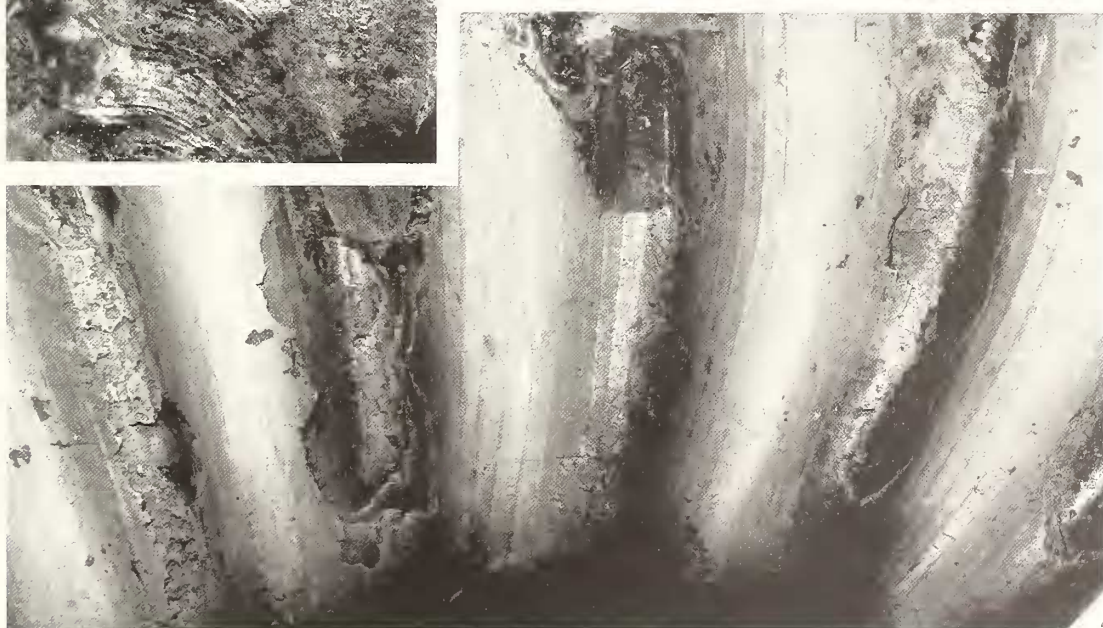
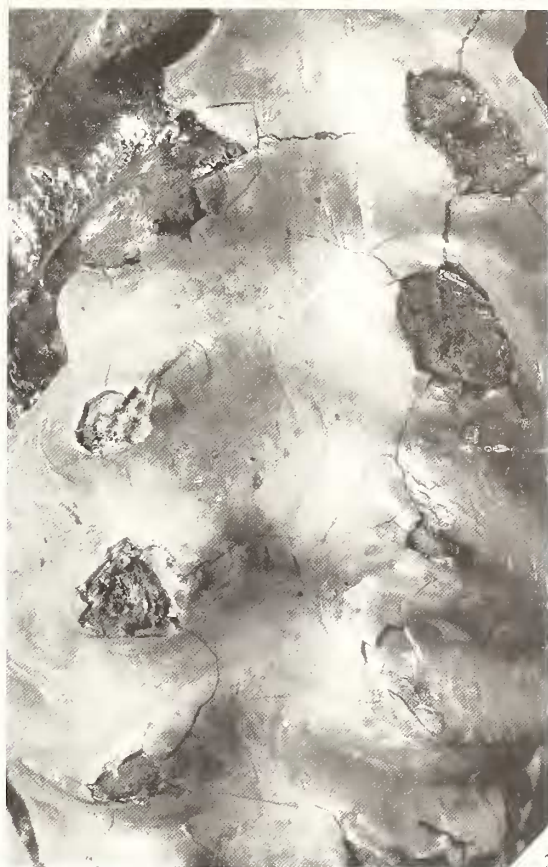
EXPLANATION OF PLATE 6

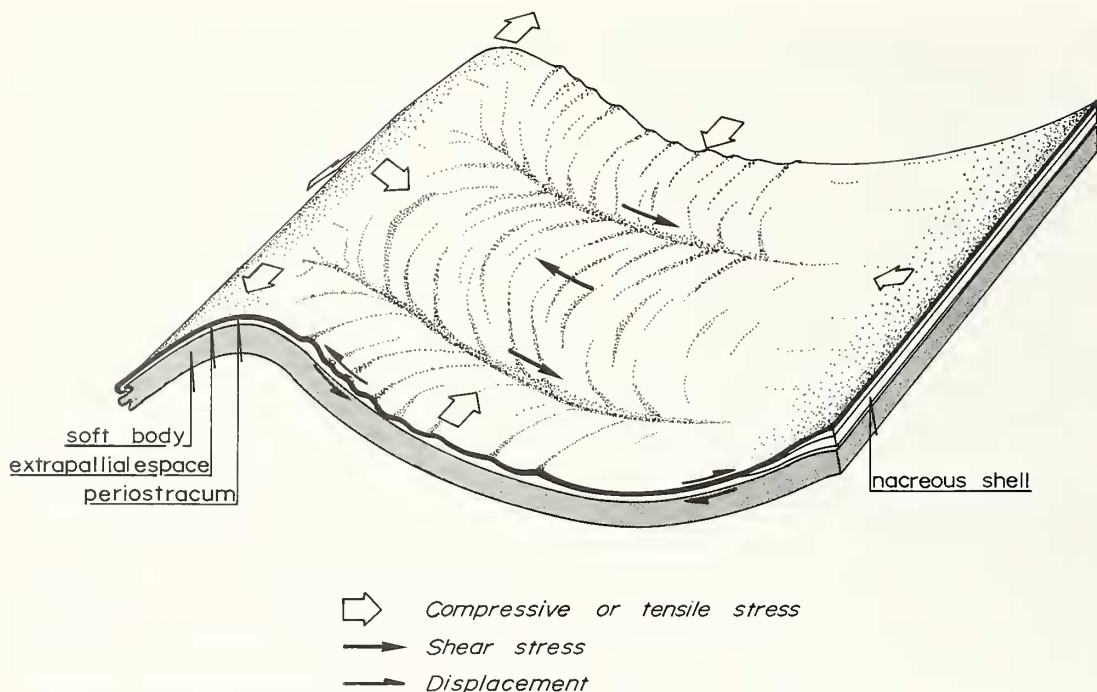
Figs 1–2. *Hoplites dentatus* (Sowerby). Natural History Museum, C88627; Devizes, Wiltshire; Albian; ventral view, aperture to the top; ventral sinuous wrinkles at the bases of ventrolateral tubercles; $\times 3$.

Fig. 3. *Placenticerus umkwelanensis* Klinger. Natural History Museum, C93898; Mfolozi and Umkwelane Hill area, Zululand; Coniacian; left view; typical feather-like ornament; $\times 4$.

Fig. 4. *Arietitidae* sp. Natural History Museum, C41785; Timsbury, near Radstock; Lower Lias; right view; growth lines between growth increments appear in low-relief at the intercostal valleys (light areas) and, usually, in high-relief at the ribs (dark bands); $\times 3$.

All specimens uncoated.





TEXT-FIG. 3. Inferred distribution of stresses during the process of contraction and folding of the uncalcified periostracum of ribbed ammonites. Tensile radial and longitudinal stresses developed at the rib, whereas the intercostal valley was compressed radially (if radial shortening occurred) and longitudinally. Shear stresses arose between longitudinal lines of attachment (in low-relief) and intermediate areas, with the formation of adorally convex wrinkles. Formation of sinusoids also led to minor displacements between periostracum and soft body. Growth direction is to the left. Although mainly based on *Hildaites* (see Pl. 2, figs 2–3), the figure is intended to represent a general case.

in much the same way as that described by Linsley and Javidpour (1980) in some gastropod families in which lamellae between constrictions are similarly arranged. Although I only describe the case of *Pavlovia*, this pattern could probably be applied to many other constriction-bearing shells. Future work is needed in this respect.

Apertures, ribs and constriction: functional aspects

Both for hildoceratids and pavloviids the creation of a thin, scarcely resistant shell could have been adaptive. An easy-to-tear aperture would have allowed the animal to get free from benthic predators gripping the aperture during the subjugation phase (e.g. decapod crustaceans; see Lehmann 1981; Ward 1981) with minimal shell losses. Then the ammonite was able to swim out of the reach of the predator. It should be stressed that four out of seven specimens of Hildoceratinae (57 per cent) displayed repaired apertures. Note that these features were not transmitted to the mould. This mechanism makes sense only if the ammonite also had the ability to retract more or less deeply inside the shell; this could have been the case with ammonites, judging by the internal position of the mouth complex in *Arnioceras* (Lehmann 1971) and, coincidentally, *Hildaites* (Lehmann and Weitschat 1973). A similar attitude of passive defence was supposed by Lehmann and Kulicki (1990, fig. 2) from the study of aptychi. As soon as hildoceratids reached maturity and

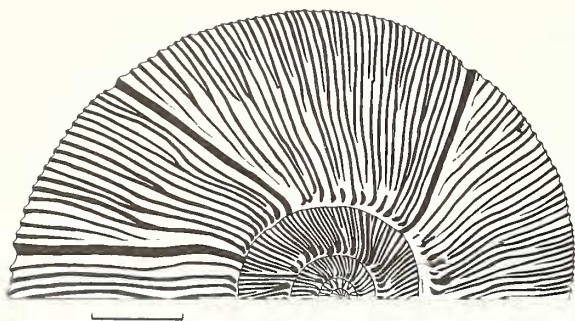


TEXT-FIG. 4. *Pavlovia* sp. Oxford University Museum, J35891; Hartwell, south-west of Aylesbury, Buckinghamshire; Portlandian. Shell section through a constriction (c) and subsequent rib (r). Nacreous lamellae wedge out at the adoral slope of the rib, whereas lamellae corresponding to the next secretion cycle can be seen emerging at the inner side of the rib (bottom left). Growth direction is to the left. Composite scanning micrograph; $\times 70$.

thickened the definitive aperture, and when *Pavlovia* made a new constriction, the strategy became a very different one, that of resistance to shell breakage and peeling (see Kennedy and Cobban 1976). In this way, apertures could have played two defensive roles depending on the state of calcification.

Therefore, the major function of ribs strictly as reinforcement of the very apertural margin, invoked by Kennedy and Cobban (1976) and Checa and Westermann (1989), is at least debatable, as soon as submature stages are concerned. Rather, they must have prevented peeling of the shell some distance from the aperture backwards.

Constrictions do not usually coincide with the preceding costae and are more forwardly inclined (Checa and Westermann 1989), this being especially true for involute shells. The next ribs immediately after the constriction are always parallel to it. In general it seems as if the aperture deviated progressively from its ideal orientation (relative to shell radius) and was reorientated at the constrictions. This could be true in the strictest sense since longitudinal shortening due to folding of the periostracum must have been more intense towards the venter, as in this zone the periostracum is more repeatedly folded (except for simple ribs). In this way a progressive change in aperture orientation could have taken place, which was compensated at the constriction. This deviation grew with the interval between constrictions. Involute shells display the greatest differences between the internal (umbilical) and external (ventral) spiral lengths and, at the same time, they display the greatest ratio of secondary or intercalary to primary ribs, since corrugations tend to have a uniform distribution along the shell (Checa and Westermann, 1989). The involute ammonite *Maorites* displays spectacular examples of intersection between ribs and constrictions (Text-fig. 5; for other examples, see Macellari 1986), and it can be seen how ribs become



TEXT-FIG. 5. Ribs and constrictions are non-congruent in *Maorites seymourianus* (Kilian and Reboul). Drawing of specimen in Macellari (1986, fig. 30/1, 2). Scale bar is 20 mm.

progressively deviated only from the division point to the venter, while primary ribs retain the same orientation. In the widely-umbilicated, multi-constricted *Pavlovia*, ribs and constrictions are similarly directed. This implies that non-constricted shells with divided ribs had to avoid apertural deviation in some way. They could have achieved this by folding the primary rib in a long-wave and high-amplitude fashion, as in *Rasenina* (see below and Text-fig. 6C), which accounts for the well-known fact that primary ribs are usually much more developed than their corresponding secondary ribs in many groups of ammonites.

As an additional advantage, corrugation of the viscoelastic soft body and of the periostracum led to sinusoidal folds. This is the strongest shape in compression, since having permanent and more or less constant curvature, it is the least prone to develop local bending (Gordon 1978; Wilmot 1990). Ammonite rib profile and distribution was therefore highly fitted to the protective role it had to perform. Wrinkles probably did not achieve the status of functional structures. They were rather a fabrication noise (in the sense of Seilacher 1973) arising from the very process of construction.

The exact advantages of the present concertina-like pattern of rib construction over other alternatives are not easy to determine, although it obeys a major rule: it is simple. It surely required less genetic instructions than the alternative of, for example, widening the apertural mantle periodically. This last strategy would have also obliged ammonoids to calcify each growth increment immediately after its secretion; otherwise, rib shape could not have been maintained.

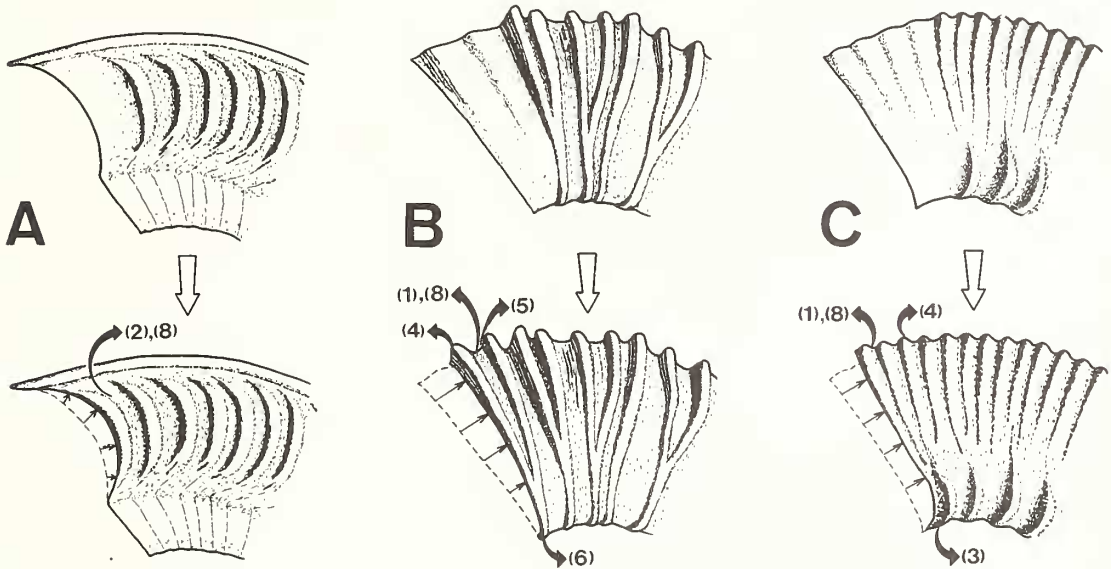
A MORPHOGENETIC MODEL FOR AMMONITE RIBS

The process of folding of the periostracum

One of the main problems concerning the present model is the morphology and distribution of the muscular part responsible for the repeated folding of the periostracum, which must have been located orally. From the available data, there are two possibilities. Folding could have been brought about by the contraction of narrow longitudinal muscles attached to the inner surface of the periostracum (leading to longitudinal lines or bands on the shell). Traction along these lines could explain adorally concave wrinkles associated with longitudinal lines (8), but not costal bulges in themselves. Additionally, growth lines do not become significantly deviated when crossing longitudinal lines of attachment, which implies that they were not effective retraction lines.

A more likely hypothesis is that more or less inert lines of attachment of the periostracum to the mantle epithelium existed, while contraction was effected by an active oral muscular area. Palframan (1969) referred to oral muscle scars from *Hecticoceras*. When folding occurred, the periostracum was compressed radially at the intercostal valleys (Text-fig. 3), originating longitudinal and adorally convergent wrinkles, according to rib shape. At the same time the periostracum was dragged backwards, but, given its flexibility, it remained slightly behind the underlying soft body epithelium at the areas between attachment lines. This gave rise to longitudinal shear stresses

between attachment lines and the areas between them. If dragging was not homogeneous along different attachment lines (as was probably the case with hildoceratins, Text-fig. 6A) shear stresses also arose between adjacent lines. Shear stresses originated by dragging of the periostracum led to the generalized formation of adorally convex wrinkles. Minor differential displacements between periostracum and the soft body also arose from the folding process, in such a way that the periostracum must have slid somewhat upslope on both rib sides (Text-fig. 3). Differential displacements created at the areas between attachment lines both by dragging and folding of the periostracum would have combined together at the apical slopes of ribs but would have counteracted each other at the adoral ones. This explains why longitudinal lines and their associated wrinkles initiate well down the adoral slope of the rib, but tend to invade the rib crest from the rear.



TEXT-FIG. 6. Proposed modes for the construction of ribs in different groups of ammonites, with indication of the kinds of microsculptures (numbers between parentheses) which are most likely to be formed in each case. Top row, prefolding stage; bottom row, postfolding stage, with prefolding outline insinuated (broken line). A, Hildoceratinae, folding was local and inhomogeneous and each folding event led to a single rib. B, *Pavlovia*, contraction affected the whole peristome inhomogeneously and a bifurcate rib was formed after a single folding event. C, *Rasenia*, *Pararasenia*, the whole uncalcified peristome contracted more or less homogeneously leading both to fasciculate secondary ribs and to a single wide primary rib. In B and C secondary ribs were already insinuated in the prefolding stage.

In summary, two different scale folds developed on the shells of ribbed ammonites. Long-wave folds (ribs) were created by muscular contraction of the soft body epithelium lining the shell, while short-wave transversal folds (wrinkles) developed exclusively on the periostracum.

Although this picture could have had a general applicability, differences in the folding process arose between different ammonites. In simple-ribbed hildoceratins it is clear that each retraction and contraction episode led to a rib (Text-fig. 6A). This was not obviously the case of ammonites with divided ribs. Traumas and abnormalities are always useful as natural experiments, and this study is not an exception. In one specimen of *Pararasenia* (Pl. 4, figs 1–2) the shell had been severely injured (peeled back) for, at least, some 30 degrees. Growth after the injury was characterized by anomalous ribs, in the sense that they were too low and too widely spaced. The most immediate

explanation is that the animal was no longer able to fold the periostracum completely or in part, since the oral muscular area responsible for this process had been bitten away. The capability to make normal ribs was regenerated some one-quarter whorl after the injury, when primary ribs reappeared. Therefore, we are possibly contemplating the shape of the periostracum in its unfolded state. This case supports the hypothesis of an active muscular area in addition to attachment lines, since here muscular contraction presumably did not take place, but attachment lines were never lost after the injury. Retraction did not occur in this *Pararosenia* by teratological reasons, leading to a deflated periostracum, with lines of attachment to the soft body rising from the background. Otherwise, contraction of the soft body would have inflated the rib, and its surface would have bulged smoothly. Note also that in the specimen alluded to secondary ribs are only insinuated, while primary ribs are totally absent during the anomalous stage. This allows me to offer an explanation for the construction of divided (fasciculated) ribs in *Pararosenia*. The body advanced the whole length of the fasciculation to be created, while secreting a periostracum which was only slightly corrugated from the middle flank to the venter (Text-fig. 6C). Then forward motion ceased and the body contracted. Several short-wavelength, small amplitude folds were created at the upper flank according to the previous smooth corrugations, while a single, long-wavelength and high amplitude fold formed at the lower flank, originating the primary rib. Calcification presumably proceeded afterwards. This can possibly be applied to other (perhaps most) genera with divided ribs. In this way, a more or less homogeneous contraction along the whorl cross-section occurred, which may explain why primary ribs are usually much more developed than their corresponding secondary ribs (which is also a common figure in many groups of ammonites) and why apertural deviation did not take place in non-constricted shells with divided ribs (see above).

The case of *Pavlovia* (Text-fig. 6B) could be considered as intermediate, since presumably divided ribs were formed according to a *Pararosenia*-like pattern, with insinuated primary ribs. Nevertheless, contraction in *Pavlovia* was not so homogeneous as in *Pararosenia*, but, judging by rib profile, contraction increased from the umbilical seam to the venter.

Conclusion: the sequence of events

As evidenced by the above features, ribs, at least for Jurassic and Cretaceous ammonites, are compressional features, i.e. they are folds in the mechanical sense of the term. Their formation cycle could be as follows (Text-fig. 6).

(1) The soft body advanced beyond the last-formed aperture while continuously secreting a periostracum. This initial layer was not at all or only slightly folded.

(2) When this periostracum was extended to the length of a new rib, retraction of the soft body took place, which was attached to the periostracum at certain lines; folding of the periostracum then occurred, giving rise to a non-calcified rib. In constricted forms, this process was repeated until a new constriction was to be formed. Then the aperture rotated slightly forward and folded once again to form the constriction and subsequent rib.

(3) Calcification of the newly-formed rib or ribs began slightly prior to, or at, the same time as a new cycle was to be initiated with periostracal growth beyond the aperture. In constricted forms a new secretion cycle did not begin until the previous shell was fully calcified.

The segmental growth model revised

When Checa and Westermann (1989) proposed the segmental growth model, they based their argument on the intuitive notion that ribs were secreted as the juxtaposition of (immediately) calcified growth increments. Therefore, they assumed implicitly that the body mantle had to widen and contract repeatedly at the apertural edge. They found a perfect parallelism between growth lines and ribs in more than 150 ammonite genera. Therefore, the peristome had to change its orientation and shape to accommodate the variable morphology of divided ribs (see their fig. 1). As stated above, this is obviously not the case, but the geometric coincidence between ribs and growth lines

makes sense also in the 'concertina' model if muscular attachment areas allowing retraction of the periostracum were distributed around the mouth. The new material also reveals that ribs are not always parallel to growth lines, since sometimes the folding axis of the new uncalcified ribs bisected growth lines at low angles. This has been observed in hildoceratins (Pl. 2, figs 2-3, 5; Pl. 3, figs 1-3), *Kosmoceras* (Pl. 5, fig. 3) and, more exceptionally, in *Pavlovia*.

THE ORIGIN OF THE FEATHER-LIKE ORNAMENT

This kind of ornament consists in a series of forwardly directed chevron-like wrinkles. It was figured and described in *Placenticerus* (Hyatt 1903, pl. 47), in Bathonian and Oxfordian oppeliids (Waagen 1869, pl. 18, fig. 5; Petitclerc 1918, fig. 1) and in *Taramelliceras* (Hölder 1955). Arkell *et al.* (1957) also referred to this ornament in examples of the Bajocian *Protoecotraustes* and the Albian *Beudanticeras* and *Brewericeras*. I have recognized feather-like microsculptures in specimens of *Tragophylloceras* (Pl. 5, fig. 4), *Oxyoticerus* and several Hildocerataceae (Pl. 2, figs 4-5) (see also Table 1).

Seilacher (1988) considered these structures to be the insertion of retractor muscles. He probably based his view on the assertion of Arkell *et al.* (1957, p. L92) that in *Placenticerus* feather structures are 'apparently confined to the structure of the inner shell layers'. This is certainly not the case, since the only specimen of *Placenticerus* with the outermost shell preserved (*Pl. meeki*, C22686 in Table 1) displays well marked feather-like wrinkles. This applies also to the other genera listed in Table 1 displaying microsculpture (2). Therefore, this rare ornament was not internal (as assumed by the muscular hypothesis), but external. In *Placenticerus* external wrinkles are easily transmitted to the inner mould surface given the extremely thin shell borne by this genus (see thickness data in Westermann 1971, fig. 7). Individual wrinkles may sometimes span the whole space between the widely spaced, low-relief ribs, although the whole pattern may be interrupted at some definite growth lines (Pl. 6, fig. 3). Nor does this figure conform to a muscle attachment model.

Additionally, feather-like wrinkles do not display homology; they are exclusive of ammonites bearing concave ribs and can be reproduced easily in laboratory experiments (Text-fig. 2B). All these facts allow me to propose a compressive origin for feather-like ornaments, as a long-wavelength variant of adorally convergent wrinkles.

GROWTH LINES IN ARIETITIDAE AND EODEROCERATIDAE

In the specimens of Arietitidae and Eoderoceratidae listed in Table 2 I have recognized a very striking feature which is not mentioned in Table 1. In these specimens growth increments are very distinctive and, importantly, the wide growth lines bounding them are low- or high-relief depending on whether they are placed at one intercostal valley or at one rib height (Pl. 6, fig. 4). Sometimes (e.g. in *Caenites brooki*) they are discontinuous in a stamp edge manner. This striking distribution could have constituted a different strategy to aid in folding the periostracum. Growth lines, which were lines of structural weakness, would have served the function of hinge lines between growth increments. Hinge (growth line) relief would have also determined the concavity of the folds, so that low-relief lines led to concave folds (intercostal valleys) and high-relief lines to convex folds (ribs). This system easily allows for radial folds to be created, but not for folds of other shapes (e.g. concave), being therefore well suited for the construction of wide radial ribs typical of arietitids and eoderoceratids. Note that two of the species listed in Table 2 also display compressive features (Table 1), although longitudinal lines (type 8) have been never found. If these ammonites lacked definite attachment lines of the periostracum to the soft body, this system of joints would have helped to fold the periostracum, thus avoiding inadequate defects. Nevertheless, observations are so fragmentary that no definitive conclusions can be reached here.

TABLE 2. List of specimens with 'arietitid-like' system of joints between growth increments (see text). All are housed at the Natural History Museum, London.

Taxon	Age	Locality	Registration No.
Arietitidae			
Arietitidae sp.	Lower Lias	Timsbury (near Radstock)	C41785
<i>Agassiceras</i> sp.	Sinemurian	Weston on Avon (Gloucestershire)	C16532
	Sinemurian	Pebworth (Gloucestershire)	C17455, -6
<i>Euagassiceras resupinatum</i> (Simpson)	Sinemurian	Pebworth (Gloucestershire)	C16269
<i>Asteroceras confusum</i> Spath	Sinemurian	Bredon (Worcestershire)	C2223
<i>Caenisites brooki</i> (Sowerby)	Sinemurian	Lyme Regis (Dorset)	C1926, C47352, C75386
	Sinemurian	Charmouth (Dorset)	C56997
Eoderoceratidae			
<i>Xiphoceras</i> sp.	U. Sinemurian		C3710
<i>Microderoceras birchi</i> (Sowerby)	Sinemurian	Lyme Regis (Dorset)	C135

TUBERCLES AND RIBS: TOWARDS A FABRICATIONAL TERMINOLOGY

Tubercles are usually the remains on the internal moulds of longer spines which were closed-off at their base. Together with ribs and keels, tubercles are one of the most common kinds of ornament in ammonoids. The only previous documented study on tubercle fabrication is, to my knowledge, that by Checa and Martín-Ramos (1989), in which the mode of growth of spines in two aspidoceratid genera (Upper Jurassic Ammonitina) is described (see their text-fig. 4). In *Aspidoceras* the long, delicate spines began as a horseshoe-shaped invagination at the shell aperture (i.e. parabolic node-like structure); the subsequent addition of incomplete, distorted rings of shell gradually formed a hollow, slightly conical spine which remained open at its tip. Spines could continue to grow even when the mantle moved forward beyond the tubercle limits. This pattern is similar to that reported for some Recent and extinct bivalves and gastropods. *Orthaspidoceras* has one periumbilical row of mammiform spines which grew at the same time as the mantle moved forward by the consecutive addition of protuberant waves of shell increments at the aperture. Therefore, there was no single mode by which ammonite spines were formed.

Even though ribs and tubercles may coexist on the same shell, it is clear that they are morphogenetically unrelated, that is, a fabrication continuum between both kinds of structures can hardly be envisaged. Therefore, the terms proposed for ammonoid ribbing by Arkell *et al.* (1957, pp. L90–L91) can be grouped into two classes on a fabrication base. Structures fabricated in a tubercle-like fashion would include spines, clavi and nodes (also parabolic nodes). Rib-related structures are plications, and bullae.

Acknowledgements. I am specially indebted to Mr H. P. Powell (University Museum Oxford) and Mr S. Baker (Natural History Museum, London). Both of them guided me patiently through the collections of their respective institutions. This research was greatly helped by the loan of selected specimens of the Oxford University Museum. My colleagues, Drs J. Rodríguez Fernández and A. P. Jiménez Jiménez, and Mr Harry Taylor (Natural History Museum) took the photographs or helped with them. Dr J. Soria (Department of Geology, Univ. Alicante) kindly designed Text-figure 3. Drs C. Sanz de Galdeano and J. C. Balanyá (Department of Geotectonics, Univ. Granada) advised on folding mechanics and Drs J. Sandoval and M. Company (Department of Stratigraphy and Palaeontology, Univ. Granada) revised the manuscript. This